First Records from Wellington Caves, New South Wales, of the Extinct Madtsoiid Snake *Wonambi naracoortensis* Smith, 1976

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Two trunk vertebrae of a species of *Wonambi* (Serpentes, Madtsoiidae) from unknown deposits in the Wellington Caves system are the only specimens of this taxon known from New South Wales, and considered to be Pleistocene in age. The specimens are referred to the type species, *W. naracoortensis* Smith, 1976. Together with other known occurrences of the genus (in South Australia and Western Australia), this record supports an hypothesis of association with temperate climates during the Quaternary. Other specimens previously referred to *Wonambi* are reassessed with implications for the distribution of *Wonambi* and another large madtsoiid, *Yurlunggur* Scanlon, 1992.

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INTRODUCTION

The two specimens described here have somewhat different histories, although both were collected from unknown deposits in the Wellington Caves system, and both passed through the hands of Jack Mahoney (University of Sydney, Geology) as well as the collections of the Australian Museum (AM). During work by the author on the AM vertebrate fossil collection in 1987, several small lots of unregistered material came to light which, as indicated by handwritten labels, had been collected from Wellington Caves by Mahoney *et al.* during the 1960s. In one of these was a single large vertebra showing characteristic features of the extinct family Madtsoiidae (described as a subfamily of Boidae by Hoffstetter, 1961, but treated as a distinct family by McDowell, 1987 and Scanlon, 1992, 1993). A second specimen was located by Paul Willis in the collections of the Department of Geology and Geophysics, University of Sydney, in a batch of Wellington material which appears to have been collected prior to 1915, most probably in Gaden Cave, and later set aside from the rest of the collection by Mahoney (Willis *et al.*, 1992). After comparison with the published descriptions of *Wonambi naracoortensis* Smith, 1976 and other madtsoiids, vertebrae of *Wonambi* from Naracoorte, and Tertiary material of related taxa from several northern Australian sites, there seems no reason to distinguish the Wellington specimens taxonomically from *W. naracoortensis*.

FAMILY MADTSOIIDAE HOFFSTETTER, 1961
WONAMBI NARACOORTENSIS SMITH, 1976

The first vertebra has been registered as F72999 in the AM palaeontological collection. The only data on the handwritten label with the specimen are 'Stephenson and Mahoney 1962'. Neville Stephenson (pers. comm.) (now retired from the staff of the

University of Sydney, and living in the U.K.) recalls one occasion to which this could refer, but was not otherwise familiar with Wellington Caves and unable to provide any details of the site(s) from which the material came. Jack Mahoney died in 1985. If any further details of collection and stratigraphic provenance exist, they are not presently known. Other skeletal material with the same data include a dingo skull (*Canis familiaris dingo*) and several marsupial species, but it would be unwarranted at present to assume that all this material is of the same age or comes from the same deposit.

The vertebra is a middle thoracic, within the size range of the holotype and paratypes of *Wonambi naracoortensis* from Victoria Cave (Smith, 1976, table 1). It is damaged but has most features represented nearly intact on one or both sides. Two paracotylar foramina, and a single distinct parazygantral foramen, are present on each side. The neural spine is broken near its base, and the hypapophysis is also practically missing (but can not have been very wide), the ventral surface of the centrum showing an area of damage suggesting a single shear fracture. The paradiapophysis on the right side is practically absent, also apparently sheared off, but the bone surface is preserved almost intact on the left.

The preservation appears appears similar to that of the Victoria Cave specimens examined (South Australian Museum P16166 and P16170b): no secondary mineralisation or deep staining is apparent, and some of the broken faces appear quite fresh. Most of the neural spine being broken off, the internal sinus of the neural arch is exposed; it contains a network of struts like the long bones of birds. The base of the broken paradiapophysis shows a more spongy structure as seen when these processes are only slightly worn; the break on the ventral surface shows that the base of the hypapophysis, while still containing spaces and channels, is more solidly constructed.

The second specimen was located in the collections of the Department of Geology and Geophysics, University of Sydney, by Paul Willis, who recognised it as possibly *Wonambi* and brought it to my attention. It has also been transferred to the AM collection and is registered as F92050. The original handwritten label with this batch of material (also including extinct, characteristically Pleistocene mammals) appears to have read 'New Cave, Wellington' which is considered most probably to refer to Gaden Cave (Willis *et al.*, 1992). The age of the snake fossil is probably similar to that of the other material, thus Pleistocene.

This is a smaller vertebra (Fig. 1) representing a more posterior part of the trunk, probably from a snake of about the same size (neural canal height, which appears to be less strongly dependent on vertebral position than other dimensions, is similar in the two specimens; Table 1). It is similarly preserved, but more complete than the other: only the neural spine and right postzygapophysis are broken off. The keel of the neural spine extends close to the anterior edge of the zygosphene. The paradiapophyses are conspicuously wider than the zygapophyses, their smooth surfaces almost intact; the strongly convex diapophysis and flat parapophysis are additionally set off from each other by a constriction of the posterior edge. There is a distinct concavity in the dorsal edge of the diapophysis (in lateral view), which appears to be typical and rather distinctive for this species. Distinct paracotylar, parazygantral, zygantral, upper and lower lateral, and subcentral foramina are present. There are also regions of scattered small pits (as in the type material; Smith, 1976, p. 43 and fig. 2). These occur lateral and dorsal to the paracotylar and parazygantral foramina, dorsal to the diapophyses, at the base of the neural spine in the middle of the vertebra's length; and across the midline, on the dorsal surface of the zygosphene, below the cotylar rim and posteriorly on the hypapophysis. In contrast to mid-trunk specimens, the haemal keel is well defined laterally by subcentral grooves or lymphatic fossae (La Duke, 1991; cf. Smith, 1976, fig. 2) and is not developed as 'paired hypapophyses' either as in the holotype or as in posterior trunk vertebrae of *Yurlunggur camfieldensis* (Scanlon, 1992, fig. 1). A weak but distinct narrow keel is present in the midline, strongest in the middle of the vertebra, between the subcentral foramina; these are

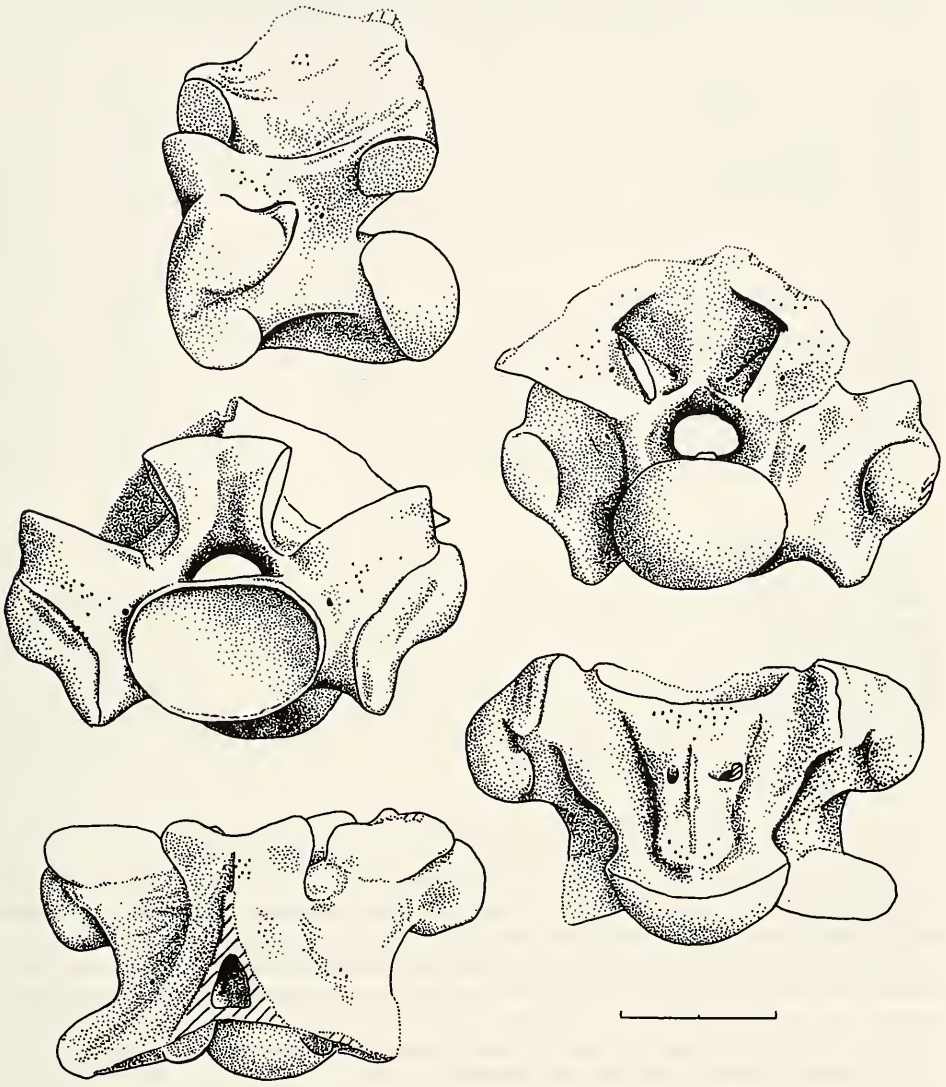

Fig. 1. Posterior trunk vertebra of *Wonambi naracoortensis* from Wellington Caves (?Gaden Cave), NSW (AM F92050). From top: lateral, posterior, anterior, ventral and dorsal views. Scale bar equals 1 cm.

the largest of any on the vertebra, lie close to the midline and open anteriad.

Table 1 gives linear measurements of both vertebrae, which allow comparison of proportions with the type series (Smith, 1976).

TABLE 1

Dimensions (in mm) of *W. naracoortensis* vertebrae from Wellington Caves, New South Wales. An asterisk indicates the measurement is affected by damage to the specimen, and would originally be greater.

	F72999	F92050
Length between zygapophyses	20.75	16.25
Maximum height (condyle-neural spine)	34.50*	24.05*
Width across prezygapophyses	33.95*	26.95
Width across paradiapophyses	32.60*	30.20
Width across postzygapophyses	33.30	26.50
Minimum width of neural arch	25.70	18.00
Zygosphene width	13.00*	9.65
Zygantrum width	15.95	10.30
Condyle width	13.80	11.45
Condyle height (oblique)	12.20	8.65
Cotyle width	14.10	12.55
Cotyle height	10.85*	9.30
Centrum length (cotyle-condyle rim)	14.55	12.20
Neural canal height	3.95	3.85
Neural canal width	7.20	4.55
Neural spine — paradiapophysis	34.55*	25.95*
Cotyle — zygosphene height	24.70	18.80
Zygosphene — condyle (oblique height)	31.40	23.60
	(L / R)	(L / R)
Prezygapophyseal facet width	6.25 / 6.20	4.20 / 4.70
Prezygapophyseal facet length	11.55* / 11.70	8.90 / 8.80
Postzygapophyseal facet width	6.20 / 6.40	4.50 / —*
Postzygapophyseal facet length	10.70 / 10.60	8.85 / —*
Zygosphenal facet width	5.00 / 4.75*	3.50 / 3.60
Zygosphenal facet length	6.70* / 8.30	5.65 / 5.70
Zygantral facet width	4.60 / 5.00	3.00 / 2.95
Zygantral facet length	8.10 / 7.70	5.75 / 5.70
Paradiapophysis facet width	6.60 / —*	6.90 / 6.65
Paradiapophysis facet length	14.70 / —*	12.00 / 12.00

OTHER PLIOCENE AND PLEISTOCENE RECORDS

Pledge (1992) records about twenty vertebrae and some jaw fragments of large madtsoiid snakes (referred to *Wonambi* sp. cf. *W. naracoortensis*) from the Curramulka Local Fauna, Corra Lynn Cave, Yorke Peninsula, South Australia. This fauna is thought to be probably early Pliocene in age (i.e. several million years older than known *W. naracoortensis*), and to be drawn from a forested habitat (rodents, bandicoots and grazing herbivores are absent; Pledge, *ibid.*). When I examined some of the material in 1990, I concluded only that *Wonambi* was definitely present. One of the specimens figured by Pledge (SAM P26535, fig. 3a), from the middle to posterior trunk, has a high neural spine and is probably *Wonambi*. However, the fauna may also include *Yurlunggur*; SAM P29908 (*ibid.*, fig. 3b; posterior trunk vertebra) appears very similar to *Yurlunggur camfieldensis* (cf. Scanlon, 1992, fig. 1E). (But it is not possible to identify snake vertebrae positively from a single illustration; *five* views are required for adequate description.) The Curramulka madtsoiid material should be studied further, as it may indicate sympatry between large species of *Wonambi* and *Yurlunggur*.

Pledge (1992) reports *W. naracoortensis* from the 'Plio-Pleistocene Kanunka Local Fauna of the Katipiri Sands, Lake Kanunka', South Australia. However, Tedford *et al.* (1992) place the Kanunka Fauna in the lower Pompapillina Member of the Tirari Formation, and consider it to be approximately 3.4 million years old (Pliocene). I have not seen this material, but consider it to be possibly either *Wonambi* or *Yurlunggur*.

McNamara (1990) figured a vertebra from the Late Pleistocene Wyandotte Local

Fauna, northeastern Queensland, which he correctly identified as comparable to *Wonambi* and referred to *Wonambi* cf. *W. naracoortensis*. The fauna is regarded as 'typically Pleistocene' and comparable to many similar-aged deposits of southern Australia (McNamara, *ibid.*). The single madtsoiid vertebra (NMV P186652) was well illustrated (*ibid.*, fig. 4G-K), and has been kindly provided on loan by G. McNamara.

There is a question as to its correct generic assignment; the specimen lacks the most distinctive characters (neural spine and paradiapophyses) and the haemal keel is more similar to those of posterior trunk vertebrae in *Yurlunggur* (Scanlon, 1992, fig. 1D-E) than to available specimens of *Wonambi*. Provisionally I refer it to *Yurlunggur* sp. If this identification is confirmed, it represents the latest known record of *Yurlunggur*, which is otherwise known from possible late Oligocene to middle Miocene of northern and central Australia (Scanlon, 1992; pers. obs.).

Lydekker (1888) listed six 'large' snake vertebrae in the British Museum (Natural History) collections (BM(NH) 42682) from Pleistocene deposits in the Wellington Caves system; these were regarded as pythonine, differing from *Morelia* but 'agreeing closely' with *Nardoa schlegelii* (= *Bothrochilus boa*) except in size. Particularly considering their large (but unspecified) size, it could have been thought that these specimens might represent an earlier record of *Wonambi*, which has larger vertebrae than most pythons; but in fact the specimens under this number are of a large elapid snake (not yet identified further).

Discussion

Wonambi naracoortensis was the first non-pythonine boid (*sensu lato*) species described from Australia, now recognised as a member of the extinct Gondwanan family Madtsoiidae. Other madtsoiids are now also known from a number of Tertiary faunas in northern Australia (*Yurlunggur camfieldensis* Scanlon, 1992 from Bullock Creek, N.T.; species of *Alamitophis* and *Patagoniophis* from Murgon, Qld; and other species of *Yurlunggur* and *Wonambi* from local faunas at Riversleigh, Qld.; Scanlon, 1992, 1993 and in prep.). The present record brings the number of localities for *W. naracoortensis* to five, all in southern Australia: Victoria Cave and Henschke's Cave, Naracoorte, southern South Australia (Smith, 1976; Barrie, 1990); Mammoth Cave and Koala Cave, southwestern Western Australia (*fide* Molnar, 1982); and now Wellington Caves, eastern New South Wales. These are all Quaternary deposits in limestone cave systems, mostly Late Pleistocene in age but with older and younger remains also present. In the case of Naracoorte, the other reptile species present do not appear to differ significantly from those now occuring in the same area, and include several elapids but no pythons (Smith, 1976); few reptile remains have yet been identified from the other sites (Dawson, 1985; Molnar, 1982).

W. naracoortensis is thus represented by more complete material and from a wider geographic range than any other madtsoiid snake, but its biology is still a matter of speculation rather than firm inference. Its broad southern Australian distribution in the Pleistocene can be compared with that of the extant Tiger snake, *Notechis scutatus* (Peters) (Elapidae), and suggests tolerance of cool climates, whereas *Yurlunggur*, apparently present in the south earlier but by the Pleistocene persisting only in the north, may have been less cold-tolerant.

Large madtsoiids coexisted with pythons of the genus *Morelia* in the Oligo-Miocene of northern Australia (Smith and Plane, 1985; Scanlon, 1988, 1992; Kluge, 1993), and at Riversleigh, pythons but not madtsoiids are found in cave deposits (pers. obs.). The Carpet python *Morelia spilota* (Lacépede) is today broadly distributed across southern Australia, but it has not been recorded from the cave deposits where *Wonambi* occurs. Whatever the environmental or biotic factors that drove the last madtsoiids to extinction, pythons appear to be the most direct beneficiaries of their demise.

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